A STUDY OF INFLUENCES WHICH MAY AFFECT THE SEX–RATIO OF THE DEER–MOUSE (*PEROMYSCUS*).

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Introduction.

For the past eight years the senior author has been conducting breeding experiments upon California deer-mice, chiefly subspecies of *Peromyscus maniculatus*.[1] Throughout this period, fairly complete records have been kept of the births, with a view to the ultimate use of these data in a study like the present.[2] The work of tabulating the crude data and of computing the values herein presented has been chiefly performed by the junior authors. The senior author has, however, supervised the work throughout, and assumes responsibility for the accuracy of these various figures.

The data upon which this report is based are not in all respects as complete as might be desired for the study of sex-ratios, though we do not believe that their value is seriously affected by these limitations. Thus the number of individuals in a brood was frequently not determined until the expiration of some days, or even as much as two weeks after birth. As a rule, the brood was discovered on the day of its birth, or within one or two days thereafter. The number of young was commonly recorded at that time, in cases where it was possible to do so without seriously disturbing the mother. At latest, the number was recorded about 16 days after birth, at which time we have regarded it as safe to clean out the cage and change the nesting material.

Record of the number of each sex in a brood was not usually made at the time of this first count. In some cases it was made

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[1] Sumner, 1920, and papers therein cited.

[2] There are here included a few hundred mice from the records of Mr. Huestis, and a few hundred others from the records of Mr. H. H. Collins. We are indebted to Mr. Collins for permission to use these last.

within the next few weeks; in others it was deferred until the time of marking, when the broods were broken up, those of different sex being segregated, and each individual being registered and given its proper serial number and identification mark. There has been no uniformity of practice in regard to the age at which the mice have been thus separated, marked and registered. Whenever practicable, this has been done within six or eight weeks after birth, but three months or more have sometimes elapsed before it has been convenient to do so. When, as is commonly true, no deaths have occurred during the interval which has elapsed since the first count, no harm can have resulted from thus deferring the record of sex.

A few words are worth while at this point in reference to the possible bearing which such imperfections in our records might be supposed to have upon the results set forth in this paper. As already stated, we do not believe that they seriously affect their value. In the first place, such errors as actually exist are ones of omission. The number recorded for certain broods is doubtless too small, owing to the occasional presence of stillborn young, or of ones which died within the few days following birth. On the other hand, we are confident that mistakes in the identification of the sexes have been so infrequent as to be negligible.

Regarding this matter of incompleteness of the entries, several things must be said. Firstly, it is doubtful whether any records are possible which are perfectly complete in this respect. It is a practical impossibility to inspect every brood immediately after birth, and in the interval which elapses the mother may eat such stillborn or feeble offspring as are present.

In the second place, the number of dead or defective members of a litter is small in *Peromyscus,* as compared, for example, with ordinary white mice. Stillborn young may be very common among the latter. In our experience they have certainly been rare among the former. As regards very early postnatal mortality, this is, from the nature of the case, difficult even to estimate from the data at our disposal. Reference to the death rate somewhat later in life may, however, be instructive. Of the 1,567 broods, comprising 5,050 young, which are listed in our records,

only 305 broods, or less than 20 per cent., showed any mortality whatever between the time of the first count (16 days or less) and the time of marking (60 ± days). The number of young of unknown sex which died during this interval was 384 or about seven and a half per cent. of the total.

Thus it is not possible that a differential death rate (unless very marked) would seriously affect the sex ratio of the survivors. We have, however, fully considered the possible influence of such a differential death rate, and have endeavored to determine its degree, if actual. This has been done by comparing the sex ratios in broods in which deaths (of undetermined sex) are known to have occurred with broods in which no deaths are known to have occurred (see below). Unfortunately the figures are available for only a very small number of offspring of known sex (40) which died from natural causes before the " sexing " of the broods to which they belonged.

As already stated, the total number of broods recorded is 1,567, comprising 5,050 young, or an average of 3.22 mice per brood. According to sex, these were distributed as follows:

Males 2,295
Females 2,357
Sex undetermined (dead, killed and escaped) 398

Total 5,050

For those of known sex the sex ratio (number of males per hundred females) is 97.37 ± 1.93.[1]

[1] In computing the probable errors we have employed a formula furnished us by Dr. Raymond Pearl, viz.:

$$\pm 67.45 \ (1 + R) \ \sqrt{\frac{R}{n}},$$

in which R is the number of males divided by the number of females, and n the total number of individuals concerned.

Our colleague Dr. G. F. McEwen has computed a somewhat simpler formula for the sex ratio:

$$\pm .6745 \ \sqrt{\frac{p \ q}{n}} \times 4,$$

in which p and q are the percentages of males and females respectively. This gives approximately the same values as Dr. Pearl's formula when the sex ratios do not depart widely from 100. Neither formula is accurate when the departures are very wide.

It must be stated that the probable errors employed in this paper are about

Since, as will be shown presently, there are rather wide seasonal differences in the sex ratios found by us, and since the different months are represented very unequally in our records, it is of interest to present the mean of these separate monthly ratios. This figure is 95.65.

Both of the foregoing figures are distinctly smaller than have been given by various writers for rats and mice,[1] as well as for man and some other animals.[2] In most cases a decided excess of males has been reported. Miss King (1918), for example, from the records of 2,818 white rats born in her " stock " (*i.e.,* unselected) series, obtained a sex ratio of 104.6.

Some attention should here be devoted to the possibility, already referred to, that the sex ratio which we have obtained for *Peromyscus* has been influenced by differential mortality. As is well known, the sex ratio among stillborn infants is very high, being frequently given as 130 or more;[3] and for cattle a similarly higher prenatal mortality among the males has been reported.[4] For *Peromyscus* we have no data on this subject since the sex of stillborn young was in no case determined. As regards early post-natal mortality, also, our direct evidence is very meager, so much so as to be almost worthless. 424 deaths occurred between the date of counting and the date of marking and registration. Owing to cannibalism and other causes, it was frequently impossible to determine the sex of these dead individuals, and in many other cases we neglected to do so; but this was done in 40 cases. Restricting our consideration to those mice which died during the first two months of life, we have 31 individuals, of which 20 were males and 11 females. From these figures one

twice as great as those which would be obtained by another formula which has been widely followed (see Pearl and Pearl, 1908), and are therefore much safer as a basis for estimates of the significance of results. Indeed it turned out that certain highly interesting conclusions which we had drawn at the outset had to be relinquished on this account. It may be added that the conclusions of certain other writers are greatly weakened if the formula here employed is substituted.

[1] King, 1911, 1918.

[2] Morgan, 1907, pp. 365–366; 1913, pp. 230–231.

[3] Morgan, 1907, p. 368; Schultz, 1918, p. 264.

[4] Jewell, 1921.

might be led to suppose that the young males were subject to a mortality about twice as great as the females. But aside from the extremely limited numbers here concerned, there are other reasons for believing that no such marked differential mortality exists in this case.

Separate computations have been made for the broods in which no deaths were recorded and for the broods in which deaths are known to have occurred. Of the former there were 1,301 broods, containing 4,081 individuals, 2,020 being males and 2,061 females. The sex ratio here is 98.01 ± 2.07.

Of the broods which are known to have sustained losses prior to marking there were 297, originally comprising 1,079 individuals. The number dying (or missing) was 438, of which 398 were of unknown sex. The surviving 641 mice comprised 312 males and 329 females, giving a sex ratio of 94.83 ± 5.06. Thus we do find a slight difference between the complete and the depleted broods, though the difference is a quite non-significant one, statistically speaking. The reasonable inference is that the mortality, during the period here concerned, is approximately equal for the two sexes. In any case, there can be no such disparity in their respective death rates as the meager record of identified dead might lead one to suppose.

Seven possible influences, which have been held by various writers, to affect the sex ratios of animals, have been considered in our treatment of the data at hand. These are: (1) season, (2) size of the litter, (3) race, (4) hybridization, (5) inbreeding and outbreeding, (6) order of birth, (7) diet. As will appear in the ensuing pages, we have some evidence that the first, second and fourth of these influences are actually effective in the case of *Peromyscus,* though perhaps in no case can this evidence be regarded as wholly conclusive. As regards the other four possible influences, the evidence is inconclusive or is quite negative.

To the foregoing list of possible factors affecting the sex ratio we may add an eighth, namely the *year.* Surprising and inexplicable as the fact may be, we have found large and sometimes significant differences between the sex ratios for certain of the years covered by our observations. Indeed these differences are

statistically more certain than any of the others which appear in our records. Such a relationship is not, of course, an ultimate fact, incapable of further analysis. But it does not seem to be dependent upon any of the other agencies for whose influence we have positive evidence, nor are we at present able to offer even a plausible explanation of it.

We shall consider, in turn, the supposed influences which have been enumerated above.

Season.

Before proceeding to discuss the possible influence of season upon the sex ratio of *Peromyscus,* it should be stated that the mice in question have, with a few exceptions, been born and reared under atmospheric conditions closely approaching those of the outside world. The building ("murarium") used for the purpose was specially constructed with a view to securing this result throughout the year.

Our studies of the relation between season and the sex ratio emphasize the danger of basing conclusions of this sort upon inadequate statistical data, even though the results may at first seem to be "significant," according to accepted standards. Before we included the records for the last two years (1920 and 1921), the evidence of a well-marked biennial rhythm in the sex ratio of *Peromyscus* seemed fairly conclusive. The seasonal cycle, when plotted graphically, was perfectly consistent, there being an uninterrupted rise and fall twice annually. Likewise the differences between the highest and the lowest ratios were of tolerably high "significance." The inclusion of the data for these two later years greatly weakens the evidence for a definite seasonal cycle in the sex ratio. But the possibility still seems to be great enough, and the facts, if true, of sufficient interest, to warrant our presenting the evidence rather briefly.

The following table gives the sex ratio for each month of the year, likewise (in parenthesis) the number of individuals upon which this ratio is based. The table is based upon the combined data for all of the years and for all the different series of mice.

January	(185)	88.78 ± 8.92
February	(287)	90.07 ± 7.04
March	(722)	106.29 ± 5.14
April	(343)	113.04 ± 8.24
May	(506)	94.62 ± 5.63
June	(405)	87.50 ± 5.80
July	(347)	91.71 ± 6.57
August	(565)	103.97 ± 5.84
September	(445)	96.04 ± 6.13
October	(406)	107.14 ± 7.17
November	(236)	78.79 ± 6.93
December	(205)	89.81 ± 8.37

These figures and the accompanying graph (Fig. 1) reveal the existence of two annual maxima, one occurring in March and April, the other extending from August to October. Alternating with these are summer and winter minima.

It will be seen that the differences between the successive months, taken by themselves, are of very doubtful significance, while even the difference between the highest and lowest months of the year (April and November) is only a little more than three times its probable error. With the exception of September, however, the seasonal cycle presents a perfectly consistent picture, there being an almost uninterrupted rise and fall twice annually.

The dotted line in the figure is based upon the date of conception, instead of the date of birth. The date of conception has been computed, for each brood, by subtracting 22 days from the date of birth, this being the usual period of gestation.[1] Such a procedure has inevitably resulted in the transference of part, though not all of the broods to the month immediately preceding. Were the period of gestation exactly one month, the one graph would be an exact duplication of the other. As it is, they present some obvious differences of form. The chief of these is the division of the fall "maximum" into two entirely distinct peaks.

Since, for various reasons, it does not seem probable that the differences between the consecutive months should be regarded as significant, we may profitably combine our monthly birth records into four seasons of three months each. Reference to the table of monthly ratios shows that we may distinguish two high periods
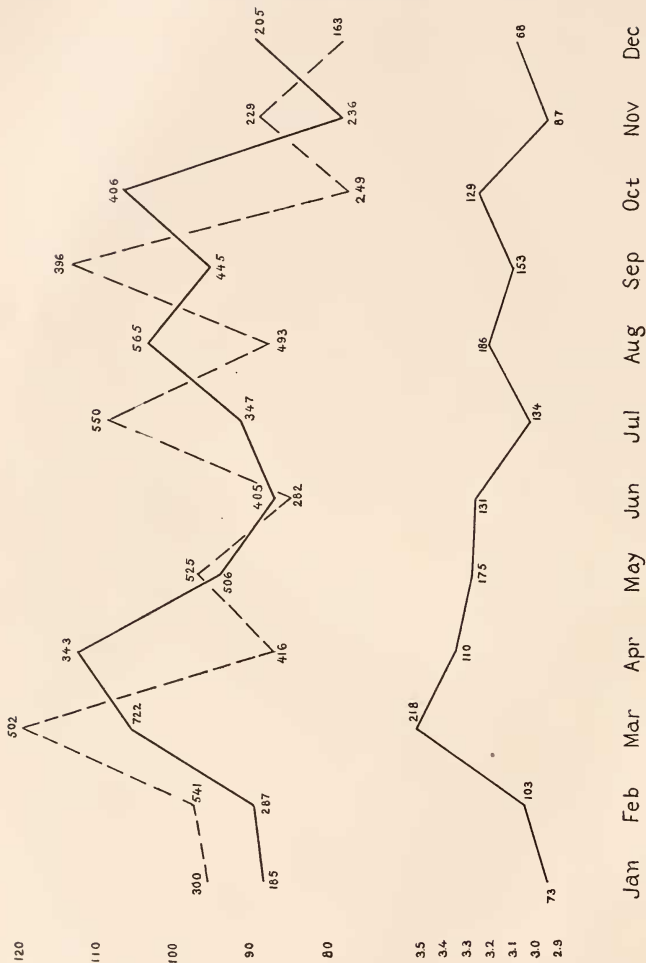
[1] Sumner, 1916.

Fig. 1. Above: the sex ratio of *Peromyscus* for each month of the year, computed from all the material. The continuous line is based upon the date of birth, the broken line upon the date of conception. Ordinates indicate sex ratios (number of males per hundred females). The figures along the graphs denote the number of individuals born (or conceived) during each month of the year.

Below: mean size of brood for each month of the year. Figures along line = number of broods.

and two low periods annually. The sex ratios for these four periods are as follows:

(1) February–April .... 104.23 ± 3.85
(2) May–July .... 91.48 ± 3.48
(3) August–October .... 102.29 ± 3.68
(4) November–January .... 85.21 ± 4.62

The greatest difference between two of these ratios is that between the first and fourth periods. This is 19.02 ± 6.01. Taken by itself, such a difference is commonly regarded as having a probable significance.

When the same broods are grouped according to date of conception, the figures become:

(1) January to March .... 105.35 ± 3.85
(2) April to June .... 91.09 ± 3.50
(3) July to September .... 102.68 ± 3.66
(4) October to December .... 82.10 ± 4.38

Here, again, the greatest difference is between the first and fourth periods, being, in this case 23.25 ± 5.83, or almost exactly four times its probable error.

Figure 2 is based upon the sex ratios for the four 3-month periods of the year, both when the broods are grouped according to date of birth and according to date of conception. The two graphs are seen to be in very close agreement, though the divisions between the 3-month periods have, in the second case, been advanced by one month.

It is when we subdivide our material into groups of one sort or another that the inconstancy of these seasonal differences becomes evident. Dividing our broods according to years is not very instructive, owing to the relatively small number born in any one year, taken singly, and particularly to the exceedingly meager records for certain months. These graphs (not here reproduced) show various extreme fluctuations which must be regarded as purely accidental. Five[1] of the seven "curves" show, however, what may be regarded as spring and fall maxima, though the position of these varies somewhat from year to year. Two of

[1] Those for 1915 to 1919 inclusive, 1920 and 1921 being the exceptions. No graph is possible for the first year (1914) owing to the small number of months represented in our records.

them, on the contrary (including one of the fullest years) give little indication of such relations.

More instructive are the results of combining these years into three groups of two to three years each, and plotting the seasonal cycle from the combined data for each of these groups (Fig. 3). The resulting graphs require no further discussion.
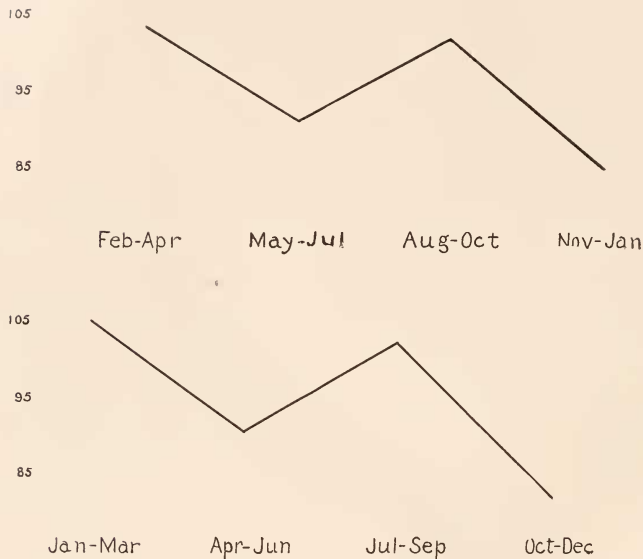

Fig. 2. Sex ratio graphs obtained by combining monthly records into "seasons" of three months each. The lower graph is based upon date of conception, the upper upon date of birth.

The data for the separate years were also grouped into 3-month periods, and graphs plotted for inspection (not reproduced). In 6 cases out of 7, there was a well-marked fall from the first to the second period, just as in the lot as a whole (Fig. 2). In 6 cases out of 7, likewise, there was a rise from the second to the third period. In only 3 cases out of 7, however, was there a fall from the third period to the fourth, one line remaining horizontal and the other three rising. (One of these last is based upon only 19 individuals.)

Two other methods of subdividing our material have been em-
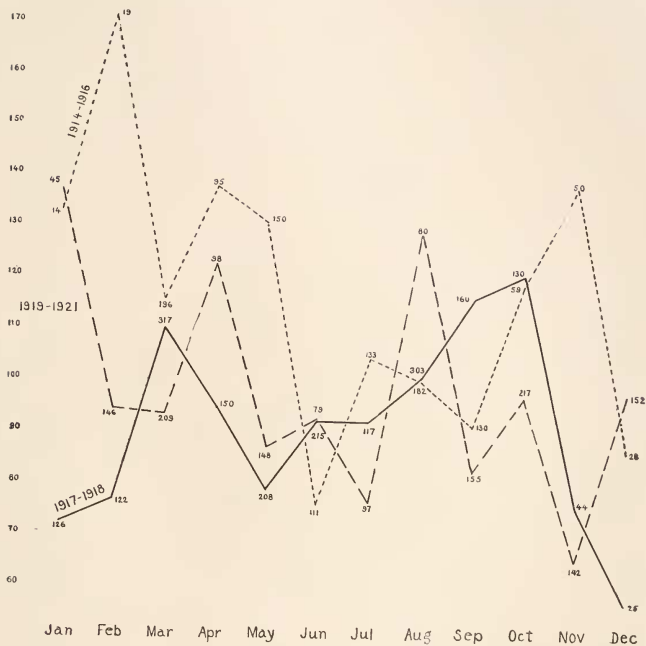ployed, these giving conflicting results. When we plot separately

FIG. 3. Seasonal variations in the sex ratio, for three groups of years,
treated separately. The continuous line (1917–1918) is based upon the largest
number (1,917). Ordinates indicate sex ratios. Numbers along graphs indi-
cate numbers born in each month. Certain of the larger fluctuations will be
seen to be due to limited numbers of individuals (*e.g.*, in 1914–1916).

the hybrid mice and those of pure race (Fig. 4), we find that
each of these groups displays a pretty well marked biennial
rhythm. This is, however, much more pronounced in the for-
mer group than in the latter, and it is also to be noted that the
" fall maximum " occurs in one case in August, in the other in
October. In passing, let us point to the distinctly higher sex
ratios shown by the hybrids throughout most of the year, a fact
to which we shall refer again.

Our material was likewise subdivided according to the size of the brood, the seasonal cycles for broods of one to six individuals
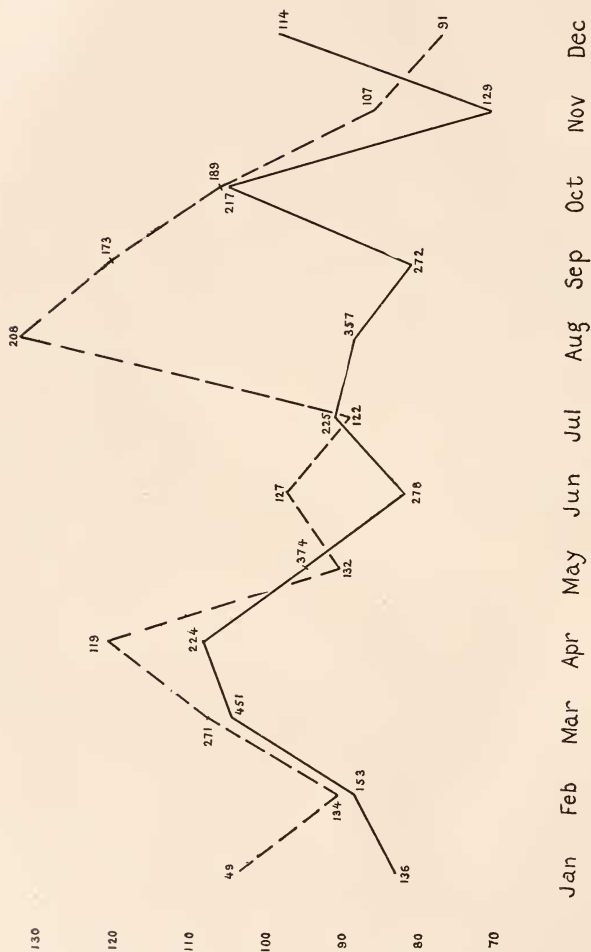

Fig. 4. Seasonal variations in the sex ratio for pure and hybrid stock, treated separately. Continuous line = pure. Broken line = hybrids.

respectively being plotted separately. Here again, the numbers
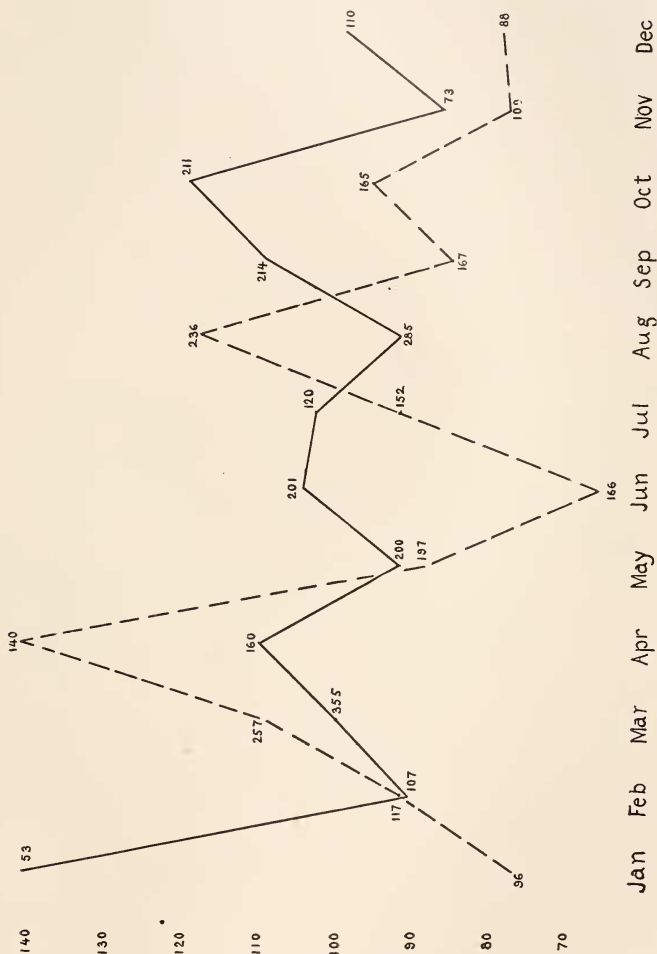comprised in some of these groups were so small that the graphs

FIG. 5. Seasonal variations in the sex ratio, for small (1 to 3) and large
(4 to 9) broods respectively. Continuous line = large. Broken line = small.

as a whole were rather confusing. We have, however, combined the data for small broods (one to three individuals) and for large broods (four to nine individuals) respectively (Fig. 5). This gives us two groups, each comprising about half of our material. The former group exhibits a very pronounced biennial rhythm with maxima in April and August.[1] The curve for the latter group, however, although based on somewhat greater numbers than the first, agrees only in having a well-marked fall maximum (September–October), with lower ratios in the summer and winter. There is but slight evidence of a spring maximum, and there are other irregularities in the " curve " for this large subdivision of our material. In general, none of these differences are of probable statistical significance. The high point in January cannot be regarded seriously, owing to the small number of individuals (53) for that month.

It must be conceded that the differences in the seasonal cycle, shown by these two groups of mice, seriously weaken our evidence for the existence of significant seasonal differences of any sort. For it does not seem likely that mice belonging to broods of different sizes actually behave differently in this respect.[2] It seems more likely that, for present purposes, we have two random samples of the population.

However, the fact stands that considerable differences have been found in the sex ratios of *Peromyscus* at different times of the year, whether or not these differences are due to " chance " (*i.e.*, errors of random sampling). Let us grant, for the moment, that the differences are not accidental. It then remains to consider whether they are due to season *per se*. It will be shown below that our hybrids as a class give considerably higher sex ratios than do the mice of pure strain. Also, quite independently of this last, it will be shown that mice born in different years differ widely in their sex ratios. The question arises: Can it be possible that the seasonal differences which we find are due either to the unequal distribution of hybrid and pure-bred mice through-

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[1] The difference between the figures for April and June is more than four times its probable error.

[2] Even this is not impossible, however, for there is some evidence (see below) that smaller and larger broods differ in their mean sex ratios.

out the twelve months, or to the unequal part which the mice of different years may have had in determining the various monthly ratios?

The first of these possibilities is set aside by reference to Figure 4, showing the seasonal cycles of the pure and hybrid stocks plotted separately. The second we have tested by ascertaining the actual effect of each year's quota in determining the sex ratio for each of the twelve months.[1] But an examination of these figures (which it is not worth while to present here) does not support such an explanation of our seasonal cycle. Unless, therefore, all of these monthly differences are due to errors of random sampling, they are probably caused in some more or less direct way, by seasonal changes of temperature or some other physical agent.

The findings of certain other investigators regarding seasonal differences in the sex ratio may be appropriately considered here. King and Stotsenburg (1915) have presented data from 7,619 white rats reared at the Wistar Institute. The exact temperature conditions existing in the animal quarters are not discussed by the authors, though it is stated that the provisions for heat regulation were inadequate, and that the rats suffered greatly from heat during the summer months. It may be presumed that the rooms were heated to some extent during the winter.

When grouped by months, the entire data of King and Stotsenburg show what might be construed as a biennial rhythm. As regards the position of these annual maxima and minima, their results are in some respects in direct contradiction to ours. One well-defined maximum covers the period from June to August, another, the period from October to December. Minima occur in March and September. The second of these is of brief duration, being bounded on either side by months having high sex

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[1] A new set of monthly ratios was computed as follows : For each month, the number born in each of our years was multiplied by the general sex ratio for that year, and the sum of these products was divided by the total number born in that month. If the monthly differences which we have discussed above were due to the different seasonal distribution of the mice born in different years, this new set of monthly ratios ought to show much the same relations as the set computed earlier.

ratios. The former, on the other hand, is ʹʹerely the lowest point
in a prolonged period of low sex ratios.

When plotted according to 3-month periods, the records of
King and Stotsenburg show an annual minimum in the spring
(March to May) and an annual maximum in the summer (June
to August), while an intermediate condition is indicated for both
fall and winter.[1] Our figures, on the other hand, show maxima
in the spring and fall, minima in the summer and winter, though
the " seasons " adopted by us commence a month earlier than
those adopted by the former authors.

The marked differences found between the seasonal cycles of
Peromyscus and the white rat might plausibly be attributed either
to the difference of species or to differences in the environmental
conditions under which the two sets of experiments were con-
ducted. On the other hand, it appears to us that the reality of
the seasonal cycle described by King and Stotsenburg is subject
to exactly the same doubts as that described by us. The fact that
the two groups of years into which the rat experiments were
divided gave quite contradictory relations for the winter months
certainly gives us reason for such skepticism.[2]

Heape (1907) gives evidence for the existence of seasonal dif-
ferences in the sex ratios of dogs. The records for nearly 18,000
greyhounds show sex ratios which fluctuate irregularly between
111 and 128 during the months of January to September inclusive.
In October, however, the curve rises to 145, in November to 180,
and in December to 195. As regards the dates of conception,
these last three months become August, September and October.
For collies, on the contrary, he says that there is " no evidence
that conception at any particular time of year affects the propor-
tion of the sexes born." It must be added, however, that his
figures for the collies indicate very considerable monthly differ-

[1] The foregoing statements refer to the entire data of King and Stotsenburg.
The material is divided by the authors into two groups which are partially
discordant with one another. One of these (that for 1911–1913) gives a graph
which is almost exactly the converse of ours.

[2] It is possible, however, that unknown influences (other than random sam-
pling) caused differences in the sex ratio from one year to another. That such
annual fluctuations actually occur in *Peromyscus* will be pointed out below.

ences among the sex ratios, and that some of these differences
would seem to be of statistical significance.

For man, Heape (1909, 1909a) has compiled data, based upon
census records of the births of more than 175,000 whites and
negroes in Cuba. Unfortunately he does not give the number of
births nor the sex ratios, for every month of the three-year period
with which he deals, but only the figures for certain selected
months of each year, namely, those showing the highest and lowest
birth rates. We are therefore obliged to take Heape's conclu-
sions to a large extent upon his own authority.

There are, he tells us (1909a) two seasons of high birth rate,
a major one in July and August, and a less marked one in Novem-
ber and December. There are likewise two seasons of low birth
rate, the chief of these being in January and February, the lesser
one in September. During the periods of high birth rate, we
are told, the sex ratios are relatively low (102.9 to 105.5 for
whites; 93.3 to 104.1 for negroes). During the periods of low
birth rate, on the other hand, the sex ratios are relatively high
(106.2 to 113.0 for whites; 99.8 to 116.3 for negroes). Thus,
there are "two sharply-defined breeding seasons each year . . .
experienced by both whites and colored at the same time," one of
these being more marked than the other.

These breeding seasons, Heape contends, are not related to the
periods of the year at which marriages are most frequent. He
seeks for correlations between certain meteorological conditions
and the periods at which conceptions occur with greatest and with
least frequency. The former periods would naturally fall in
October–November and February–March, the latter in April–
May and in December. In regard to these seasonal correlations,
Heape states: " Reference to records of temperature, barometric
pressure, humidity, etc., shows that these bursts of reproductive
activity always take place at times when there is a marked change
of climate; the one in the autumn . . ., the other in the early
months of the year . . . it is obviously not a definite temperature,
but the experience of a *change of temperature* which induces this
boisterous generative activity" (1909, pp. 35, 36). Likewise,
" my tables demonstrate that the greatest excess of females is
produced at times of greatest fertility."

King and Stotsenburg likewise believe that there is a relation between breeding activity and the sex ratio. It is stated that "the rat breeds more readily in the spring than in any other season of the year, and there is a second, less pronounced, period of sexual activity in the early fall," while relatively fewer litters are produced in July and August. Their graphs show low sex ratios in the spring, followed by high ones in the summer, and low ones again in the fall. As already stated, the results for winter are contradictory with one another.

Our records for *Peromyscus* are unfortunately not adapted to revealing definite periods of increased or diminished reproductive activity, since the matings were to a large extent controlled in accordance with the demands of the breeding experiments.[1]   But it is to be noted that the seasonal fluctuations which we have found in the sex ratio of *Peromyscus* correspond as little with those reported by Heape as they do with those reported by King and Stotsenburg. The relations which Heape believes to be shown by the Cuban statistics, even if applicable to man in that particular locality, cannot be generalized for all mammals nor for all places.

It is worth remarking at this point that the differences just discussed, between our findings and those of certain other writers, are typical of the conflicting results which pervade the entire literature of sex determination.

Size of the Broods.

The 1,567 broods here recorded ranged in size from 1 to 9, though we have only nine records of broods containing over 6 young (seven of 7, one of 8, and one of 9). The mean size of all these broods was 3.22. This figure naturally varied somewhat according to the year (2.57 to 3.67), the season (2.96 to 3.53), and the race (2.76 to 3.78), etc.

The size of the litter will first be considered in relation to its possible influence upon the sex ratio. This part of our discussion

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[1] The numbers born in November, December and January are well below those born in any other months of the year, and it is likely that this fact is due, in part, to an actual slowing down of reproduction, at least under the conditions of our experiments. But it is questionable whether any other seasonal differences in fecundity can be fairly inferred from our records.

need not be long, since the correlation in question is decidedly
doubtful.   The following table gives the sex ratios for mice be-
longing to broods containing from one to 7 (+) individuals
respectively, excluding broods in which individuals of unknown
sex are known to have died, and ones of probably mixed par-
entage (dual maternity).

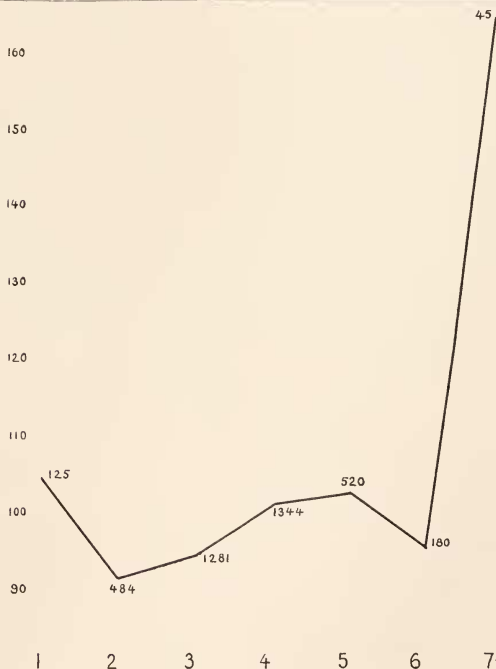| Number in Brood.	Males.	Females.	Ratio.
1	64	61	104.9 ± 12.7
2	232	252	92.1 ± 5.6
3	624	657	95.0 ± 3.6
4	677	667	101.5 ± 3.7
5	264	256	103.1 ± 6.1
6	88	92	95.6 ± 9.6
7-9	28	17	164.7 ± 33.8

Fig. 6. Variations in the mean sex ratio, according to the size of the
brood.

It will be seen (Fig. 6) that the sex ratio for broods containing from 2 to 5 individuals, inclusive, are arranged in a regularly ascending series, while the last group (7 and over) gives us a ratio far in excess of any of the others. Exceptions to this general trend are groups 1 and 6, though it will be noted that these two (as well as the last) are based upon relatively small numbers.

Despite the absolute magnitude of some of these differences, however, their statistical significance is in every case very doubtful. In most instances 'they are less than twice their own probable errors. When we combine broods of 1 to 3 and 4 to 9, inclusive, the sex ratios of these major size groups become 94.85 ± 2.94 and 102.42 ± 3.01, respectively. The difference between these values is rather less than twice its probable error. Here, then, as in the case of season, we cannot say with any confidence that the size of the brood is a factor which influences the sex ratio.

It might be inferred, moreover, that this correlation, even if actual, results from the fact that the smaller broods are ones which have been depleted by unrecorded deaths, and that the death rate has here been higher among the males. This explanation derives some support from the fact (p. 128) that among the very small number of identified dead included in our records, the males greatly preponderated. It is rendered improbable, however, by the fact (p. 129) that broods which are known to have been depleted give a sex ratio which is not significantly lower than that shown by the broods in which no deaths are known to have occurred.

Nor do our records afford any ground for the belief that these differences in the sex ratios of broods of different size depend upon the unequal distribution of such broods throughout the year. And it is equally improbable that the seasonal cycle, discussed above, is dependent upon the seasonal distribution of large and small broods. It happens that the seasonal cycle, in respect to the mean size of the brood, does correspond pretty closely, on the whole, with the seasonal cycle for sex ratio (Fig. 1). But the differences, in the former case, are so slight that they could not at most account for more than a fraction of the differences in the latter.

King and Stotsenburg obtained conflicting results from two large subdivisions of their material, when arranged to test the possible correlation between sex ratio and size of litter. The authors cautiously conclude that "the lack of uniformity in the results of this arrangement of data indicate that apparently there is no well-defined relation between litter size and sex in the albino rat."

Weldon (1907), on the other hand, believed that he had obtained some evidence that a positive correlation existed between the size of the litter and the sex ratio in mice. This relation was discernable only when the mean size of litter in different generations was considered, not being evident in respect to individual litters within a generation. The figures presented are not, however, very impressive.

Combinations of the Sexes in Individual Broods.—Thus far, the relative numbers of the sexes in broods of different size have been dealt with by methods of mass statistics. The total for each sex has been computed, and the ratio between these totals obtained. Such treatment would entirely obscure one possible phenomenon of high interest, namely the tendency of members of a litter to agree with one another in respect to sex. Do we, for example, encounter broods consisting of four or five of the same sex more frequently than would result from chance?

This question we have endeavored to answer by arranging broods of each size in groups according to the number of each sex present. For example, broods of three present four possible combinations: 3 ♂, 2 ♂ + 1 ♀, 1 ♂ + 2 ♀, 3 ♀. In table A are included only broods in which no deaths are known to have occurred. There are given the actual number of broods containing a given combination of males and females, likewise the "expected" number, to the nearest integer. In computing these last figures, it has been assumed that males and females are equally likely to be produced. The close approximation to equality in the material as a whole seems to warrant this procedure.

When we consider the comparatively small number of broods present in most of these groups, the agreement between the actual and the expected figures is remarkably close. This agreement is

Table A.

Number of Broods Containing Each Possible Combination of Males and Females.

Number in brood							
1							
Combinations	1♂	1♀					
Number of broods (actual)	64	61					
Expected number	62	62					
2							
Combinations	2♂	1♂,1♀	2♀				
Number of broods (actual)	56	120	66				
Expected number	60	121	60				
3							
Combinations	3♂	2♂,1♀	1♂,2♀	3♀			
Number of broods (actual)	53	147	171	56			
Expected number	53	160	160	53			
4							
Combinations	4♂	3♂,1♀	2♂,2♀	1♂,3♀	4♀		
Number of broods (actual)	18	88	129	83	18		
Expected number	21	84	126	84	21		
5							
Combinations	5♂	4♂,1♀	3♂,2♀	2♂,3♀	1♂,4♀	5♀	
Number of broods (actual)	4	22	27	29	17	5	
Expected number	3	16	32	32	16	3	
6							
Combinations	6♂	5♂,1♀	4♂,2♀	3♂,3♀	2♂,4♀	1♂,5♀	6♀
Number of broods (actual)	0	0	11	9	7	3	0
Expected number	0	3	7	9	7	3	0

particularly striking when we compare the actual and expected totals for all of the broods in which all members were of the same sex. The actual number of such homosexual litters, among broods containing from 2 to 6 individuals inclusive, was 276. The most probable number ,on the assumption of purely random sex-production was 274.[1] Thus, not only do we find approximately equal numbers of males and females in the population as a whole, but in single broods the distribution follows the laws of chance. There is no tendency for fetuses (or germ cells) developing in the same parents at the same time to give rise to organisms of the same sex.

It may seem, on first thought, that such evidence is conclusive against the efficacy of any factor, except the chance meeting of the gametes, which might be supposed to play a part in determining the sex ratio. On the assumption, for example, that seasonal influences of an undetermined character may affect this ratio, should we not expect undue proportions of all-male broods at one time of year, and of all-female broods at another time, and should not this fact result in a preponderance of homosexual broods throughout the year as a whole? We have not computed the proportions of all-male and all-female broods by months, but the probability of the excessive production of such broods at certain times of the year may be granted. We must, however, point out the equal probability of an excessive production of evenly balanced broods at other times of the year. During these months of average sex ratios, we should presumably have not only equal numbers of males and females produced *in the aggregate,* but a tendency toward balanced broods on the part of *individual mothers.* The possibility of sex-determining agencies other than chance combinations of the gametes in fertilization is quite unaffected by these results.

One important conclusion seems justified, however, by this utter absence of any tendency toward the preponderant production of homesexual litters. This is the non-occurrence of polyembryony or true twinning, at least with sufficient frequency to affect the results.

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1 If we include fractions (a more exact procedure) this number becomes 277. Surely this is a close " fit ! "

Newcomb (1904), from a study of 7,896 families, concluded that, after making allowance for a slight preponderance of males, the sexes in each family were distributed according to chance. There was no tendency toward an excessive production of families consisting wholly of one sex. A consideration of multiple births, however, based upon French and German statistics, showed the existence of a pronounced tendency toward agreement in sex on the part of twins and triplets. Biologists would have confidently predicted such a situation, owing to the familiar phenomenon of duplicate ("identical") twinning, but Newcomb strangely overlooked this explanation of his results and found in them support for the idea that sex is determined by unknown causes operating during development.

Race.

In the following table, the mice of "pure" (*i.e.*, non-hybrid) stock[1] are grouped according to the geographic race (subspecies) to which they belong. The La Jolla representatives of the subspecies *gambeli* are here kept distinct from those coming from the more northern localities (Berkeley and Calistoga). This is partly due to the appreciable morphological differences between these local races of *gambeli*, partly to the fact that the northern representatives were nearly all born during the months of May to August, a circumstance which may account in part for the extremely low sex ratio found in this group.

Subspecies.	Males.	Females.	Ratio.
gambeli (Berkeley and Calistoga)	49	72	68.06±8.50
gambeli (La Jolla)	770	840	91.67±3.07
sonoriensis	350	373	93.83±4.70
rubidus	150	124	120.97±9.91
Total	1,319	1,409	93.61±2.36

In making a comparison between these races, we may reasonably leave out of consideration the small group of Berkeley and Calistoga *gambeli*. The two main groups (numerically speaking), *sonoriensis* and La Jolla *gambeli*, differ from one another by an

[1] Except *P. maniculatus dubius* and *P. eremicus*, for which the numbers are too small.

amount which is less than half of its probable error. These two, however, particularly the latter, differ from *rubidus* by amounts which are possibly significant. But it is not certain that these figures imply the existence of actual racial differences in respect to sex ratio. One thing may be stated with confidence, however, namely, that the high ratio shown by *rubidus* is not due to any peculiarity in the seasonal distribution of its births. This has been shown by the following procedure. The sex ratio proper to each month, as computed for the pure races in general, has been weighted by the number of *rubidus* born in the corresponding month, and the product-sum divided by the total number of mice of this subspecies. The mean ratio thus obtained is 92.77, a figure even lower than the ratio for all mice of pure race.

The existence of racial differences in the sex ratio have been pointed out for man. According to Newcomb (1904) and Heape (1909) the ratio is higher for the white race than for negroes. Heape (1907) likewise gives different figures for different races of dogs, these figures ranging from 96 to 136. There is little analogy, perhaps, between the artificial " races " of dogs and the geographic " races " of wild mammals, and the comparison with man is of equally doubtful validity.

HYBRIDIZATION.

Of the 4,652 young of known sex, 2,930 belonged to " pure " subspecies, 1,722 to subspecific hybrids. The former were not, of course, pure, in the sense of having been closely inbred for many generations, or of being uniform in genetic composition. Their purity was relative. Among the hybrids are included, not only those of the F_1, F_2 or later generations, but various backcrosses with the parent stocks as well.[1] This procedure seems warranted, according to any theory of the behavior of subspecific characters in hybridization. There is no clear segregation of the parental stocks in the F_2 generation, as would be expected if

[1] Only subspecific crosses are here included. Crosses between "mutant" races within a subspecies, or between one of these and the parent stock, have not been regarded as hybrids for the purposes of this study. Of these, however, the number is not sufficient to materially affect the ratio for the "pure" stock, even though such an effect were known to occur.

these stocks differed by only one or by a few pairs of unit factors.
In consequence the F_2 and back-cross individuals are in a true
sense *hybrids.*

The proportions of the sexes in the two lots are as follows:

	Males.	Females.	Ratio.
Pure...........................	1,414	1,516	93.27 ± 2.32
Hybrids........................	881	841	104.76 ± 3.41

The difference between these two ratios is 11.49 ± 4.1, thus
being slightly less than three times its probable error.[1]   These
figures by themselves, therefore, cannot be held to prove at all
conclusively the existence of a higher sex ratio among subspecific
hybrids in *Peromyscus.* But the probability of such a difference
is greatly increased by several circumstances. (1) It has already
been shown (Fig. 4) that the " hybrid " ratio exceeds the " pure "
in nine months out of twelve, and that in two of the three excep-
tional cases the differences are trivial. (2) The hybrid ratio was
higher in six of the seven years, taken separately (Fig. 7), and
the single exception here is based upon a very small number of
individuals. (3) The ratios for all of the five separate groups
of hybrids are larger than that for the pure stock. (4) Such a
difference accords well with the bulk of the evidence for other
species of animals.

It is quite unlikely that the difference here found is due to any
of the other factors with which the sex ratio of *Peromyscus*
has been found to be correlated. As regards season, it has al-
ready been pointed out that this difference between the hybrid
and pure material holds for nearly all the months of the year.
Likewise the difference is very nearly the same when we deal,
in each case, with the mean of the monthly sex ratios.

Again, as regards the size of the brood, the mean difference,
in this respect, between the hybrid and pure stocks (3.26 and
3.20) is such that it could not exercise an appreciable influence
upon the sex ratio.

[1] It may be pointed out that when this probable error is computed accord-
ing to a method widely used (see p. 127), the difference is more than five
times the latter.

Nor can the differences be due to the varying proportions of these two groups which were born in different years. As already mentioned, the difference holds for six of the seven complete years of our records, the exception being unimportant, owing to the small numbers concerned. Likewise a computation analogous to that described on p. 139 shows that distribution by years (on the assumption of an equal sex ratio in hybrid and pure stock) could account for only a small fraction (2.5) of difference actually found.

Owing to the relatively small numbers, it is hardly worth while to discuss at any length the separate subspecific crosses which were made. The figures for the five different groups, with the numbers (in parenthesis) on which they are based are as follows: 114.63 (176), 114.11 (698), 97.27 (361), 95.65 (270) and 93.75 (217). Thus, all of these figures are higher than the ratio for the "pure" stock, though in the last case the difference is trivial, and in only one case is it as much as three times its probable error. Of the smallest of these figures it should be stated, however, that it is based entirely upon mice which were born from May to December, inclusive, thus missing the spring maximum.

All in all, the evidence, if not wholly decisive, points rather strongly to the conclusion that in *Peromyscus* hybridization *per se* results in increasing the proportion of males which are born.

Various previous writers have called attention to the larger proportions of males resulting from hybrid matings. To mention but a few of these cases, Guyer (1909) has presented evidence of this sort for various bird crosses,[1] Riddle (1917) for pigeons, Harrison (1919) for lepidoptera, Pearl and Pearl (1908) and Little (1919) for man, King (1911) for rats and mice. In certain of the cases discussed by Guyer and Harrison[2] the proportion of males reached 100 per cent.

[1] In some of the bird crosses discussed by Phillips (1921) the males do not seem to be in excess, but the number of individuals is small, and the data are not presented with a view to answering this question.

[2] Harrison's results are complicated by the different behavior of various reciprocal crosses in respect to the sex ratio, by the preponderance of females in some cases, and by the appearance of "intersexes," *i.e.*, intermediates between the two sexes.

Miss King gives the data for 425 hybrids (F_1, F_2 and F_3) between the Norway and the albino rat. The sex ratio found was 119.07 or 118.11, depending upon whether the entire number was included, or whether consideration was restricted to the most reliable series (277). In either case, the difference cannot be regarded as significant, according to the standard here adopted. In the first case, it is 14.5 ± 8.3.[1] Miss King has also computed the sex ratio, from the records given by von Guaita of hybrids between albino mice and Japanese waltzing mice. The ratio is 113.17, but this is based on only 356 mice of known sex, and is surely of doubtful value.

Pearl and Pearl give the results of computations, based upon vital statistics of the city of Buenos Aires. They have compared the sex ratios resulting from Argentine $\times$ Italian and Argentine $\times$ Spanish matings with those resulting from matings within each " pure " race. The figures for the " hybrid " group were in each case the larger, and the authors believed that the difference was significant in three of the four cases taken singly. But when these probable errors are computed according to the formula now adopted by Dr. Pearl (see p. 127), the significance of these various differences becomes doubtful in all cases except one. That between the sex ratio for the Italian-Argentine cross and for pure Italian stock, is 4.95 ± 1.05. In all of the other cases the probable error is half or more times as great as the difference. Despite the great numbers comprised in these statistics, there is thus some doubt as to the reality of these differences. And their biological meaning is further obscured by the fact that the " pure " races differ among themselves in respect to their sex ratios quite as significantly as they differ from the " hybrids ";[2] likewise by the fact that the highest " pure " ratio (the Spanish $\times$ Spanish) is very nearly identical with the lower of the two " hybrid " ratios. It should be added that the authors themselves did not express any great confidence that the higher ratios of the mixed matings are due to hybridization *per se*. We shall discuss later the significant yearly differences which are shown in Table I. of the

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[1] Assuming 104.6 ± 2.77 as the normal ratio for the white rat.

[2] The same reservation must, though certainly with less cogency, be made in the case of our own data, discussed above.

paper of Pearl and Pearl, though not referred to by these authors.

Little (1919) has reported upon a smaller number of offspring of "pure" and "hybrid" stocks, born at the Sloane Maternity Hospital in New York City. The matings considered were those within or between the following "races": English, Irish, Scotch, Italian, Russian, Greek, Austrian and German. Of the births of "pure" stock, there were 5,753, and these gave a sex ratio of 106.27 ± 1.81. Of the "hybrid" births there were 1,305, giving a sex ratio of 121.56 ± 4.49. The difference between these ratios is a trifle over three times its probable error. In each case still-births were included. It is of interest to note that the proportion of stillbirths among the "hybrid" matings was considerably lower than among the "pure."

If the foregoing figures represent an actual biological differ-ence between the two groups under consideration, the magnitude of this difference is surprising. For each of the "pure" races under consideration is, of course, not a race at all, biologically speaking, but is itself a hybrid mixture. The basis employed in these records was obviouslly nationality, not ethnic stock.

In a later paper (1920) Little has divided his material into "European pure," "European hybrid," "United States white," "British West Indian colored," and "United States colored." In general, the significance of Little's findings is greatly dimin-ished if the probable errors are computed according to the for-mula which has been employed in the present paper. Thus computed, these are about double the errors given by Little. But at least three of this author's differences remain of probable sig-nificance, viz.: those between European pure (104.54) and Euro-pean hybrid (122.86), between European pure (104.54) and U. S. white (118.33), and between U. S. white (118.33) and U. S. colored (96.12). It is of considerable interest that there is no significant difference between European hybrid and United States white. "This shows," as Little remarks, "that in the data studied, the United States white ratio is essentially that of a hybrid race," i.c., an even more hybrid one than the European "races."

INBREEDING.

A comparison of "inbred" and "outbred" stock (as defined below) was made at a preliminary stage of these studies, when the total number of individuals dealt with was about 1,700 less than at present. The results of this comparison were so completely negative and the amount of work involved is so great,[1] that it has not been thought worth while to revise them.

For the purpose of comparing the sex ratios, our material was divided into two classes, "outbred" and "inbred." The first class included offspring from matings between unrelated individuals or individuals not related more closely than first cousins; the second included matings between parents and offspring or brothers and sisters.

In the first class, we have 2,346 individuals, comprising 1,171 males and 1,175 females. The sex ratio is 99.66 ± 2.70. In the second class, we have 1,087 individuals, comprising 547 males and 540 females. The sex ratio here is 101.30 ± 4.07. It is obvious that this difference must be regarded as accidental. When we restrict the "inbred" group to those individuals which were derived from the matings of full brothers and sisters, the sex ratio becomes somewhat larger, being 103.56 ± 4.82. But even here, the difference between this figure and that for the "outbred" group is much less than its probable error.

Various investigators have offered data which they believed to indicate an effect of close inbreeding upon the sex ratio. It is of interest (and quite characteristic of the literature of "sex determination" in general) that some writers have found a higher proportion of males in inbred strains, while others have found the females to be in excess.

Miss King (1918), from extended experiments on the white rat concludes that inbreeding *per se* does not affect the sex ratio. Her experiments yielded, however, one important positive result, namely that strains could be selected, giving preponderant numbers of male and female offspring respectively.

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[1] It is necessary, with every brood, not only to look up the birth records but to trace out the pedigrees to some extent.

Order of Birth.

Both the order of birth, and the age of the parents have been regarded by various writers as factors in determining sex. From our data it would be difficult to separate the influence of these two factors, had we reason to suspect that either of them had any effect upon the sex ratio. Since, however, our findings here are quite inconclusive, it is a matter of no importance that the possible influence of the two factors should be kept distinct.

In 196 cases, it happened that the same parents had two or more litters of young. The sex ratio for the 554 individuals of known sex comprised in the first broods[1] is found to be 91.70 ± 5.26. That for the 627 mice in the second broods is 104.91 ± 5.65. This would seem to be a considerable difference, but the numbers are small and the probable errors correspondingly high. We are not, therefore, warranted in attaching any significance to this difference. When we add the very limited number of third and fourth broods to the second ones and compute the sex ratio for the 738 mice of known sex belonging to these "later" broods, we have 103.31 ± 5.48. The probability of an actual difference in sex ratio between first and later broods is actually diminished by this procedure.

It is of some interest that the second broods averaged somewhat larger than the first, the mean figures being 3.39 and 3.05 respectively, based upon 196 broods of each class. This difference is nearly three times its probable error.

King and Stotsenburg report for the white rat a steadily decreasing sex ratio in passing from the first to the fourth litters borne by the same mothers, the first figure being 122.0, the last 74.5. The authors recognize, however, that the number of broods under consideration does not warrant any final conclusions on this point.

Punnett (1903) from an examination of Burke's "Peerage" concludes that the first born, in man, are predominantly males.

[1] By "first" broods we here mean the first which are known to have been borne by a given mother. Since, in more than a third of the cases, the mothers were wild mice, which had been trapped when nearly or quite mature, it is likely that many of these had already given birth to young. In such cases, the actual contrast is between *earlier* and *later* broods.

Newcomb (1904) likewise finds that "the first born child of any mother is more likely to be a male, in the proportion of about 8 to 7" (p. 28).

NUTRITION.

Our data on the much-discussed subject of the relation of nutrition to the sex ratio are extremely meager, though it seems worth while to include them in this report. Any such extreme effect as has been alleged by certain writers might have been expected to manifest itself, even in the limited numbers here considered.

For the purpose of testing the possible beneficial effect of including meat in the dietary of the stock, certain lots of mice, in three successive generations, were divided into two sections, one being given a rather liberal supply of chopped, boiled meat (commonly liver), in addition to the regular ration which was strictly vegetarian, the other (control) lot being restricted to the latter. The experiment was commenced at about the time when the first of the three generations referred to was mated. The meat diet was continued until the mice of the third generation were fully grown.

In all, there were 237 young of determined sex among the offspring of meat-fed parents (second and third generations). These gave a sex ratio of 104.31 ± 9.13. In the control lot were 228 young, giving a ratio of 96.56 ± 8.61. Here, again, it is obvious that the difference is not significant. The transfer of a very few individuals from the male to the female column (or vice versa) would be sufficient to reverse it.

Cuenot and Schultze (both cited by Morgan, 1907, pp. 385, 386) performed experiments upon rats and mice, respectively, with a view to testing the possible effects of feeding upon sex determination. In neither case were significant differences found between the sets of animals under comparison, but the numbers were very small and the results almost valueless statistically. More recently, Slonaker and Card (1918) have computed sex ratios for omnivorous and strictly vegetarian white rats, finding these to be .113.6 and 107.6 respectively. Since the number of individuals and other essential matters are not stated in the brief preliminary communication referred to, we must suspend judg-

ment on the significance of these figures. Most recent experi-
ments with other animals have given negative results as regards
the effect of diet upon the sex ratio.

The Year.

We have already referred to the surprising fact that the sex
ratios of mice born in different years may differ widely and sig-
nificantly from one another. The following table gives the figures
for all the years comprised in our records, with the exception of
1914, for which the data are very meager:

	Males.	Females.	Ratio.
1915	307	306	100.33 ± 5.44
1916	262	209	125.36 ± 7.82
1917	175	248	70.56 ± 4.70
1918	758	736	102.99 ± 3.67
1919	137	116	118.10 ± 10.03
1920	121	138	87.68 ± 7.37
1921	496	560	88.57 ± 3.68

As judged by the customary standard, some of these differences
are highly significant. That, for example, between 1916 and
1917 is 54.80 ± 9.1, the difference being six times its probable
error. The chances that this result was due to " accident " (*i.e.*,
that no difference would have been found if our numbers had
been indefinitely great) are only about 23 in a million. The dif-
ference between the ratio for 1916 and the ratio for the entire
period (97.37 ± 1.93) is 3.5 times its P. E., that between 1917
and the general ratio being 5.3 times its P. E. The difference
between the largest figure (125.36) and the second smallest
(87.68) is 3.5 times its P. E., that between the smallest figure
(70.56) and the second largest figure (118.10) is 4.3 times its
P. E. The difference between the second largest and the second
smallest ratios is, however, only 2.5 times its P. E. Finally the
difference between the ratios for the two years during which the
greatest number of births occurred (1918 and 1921) is 14.42 ±
5.2, *i.e.*, it is 2.8 times its P. E.

The foregoing probabilities are, to be sure, not wholly cumula-
tive, but the conclusion seems hardly avoidable that certain of
them are real in the sense of not being due to errors or random

sampling. We must, of course, consider the possibility that these differences among the sex ratios of the various years are due to some of the other factors already considered. May they not, in part at least, be due to the unequal representation in these different years of broods born in months of high or of low sex ratio? Aside from the fact that these yearly differences are even more extreme than any of the seasonal ones, we have excluded this possibility by a procedure previously adopted in similar cases. The number born in each month of each year was multiplied by
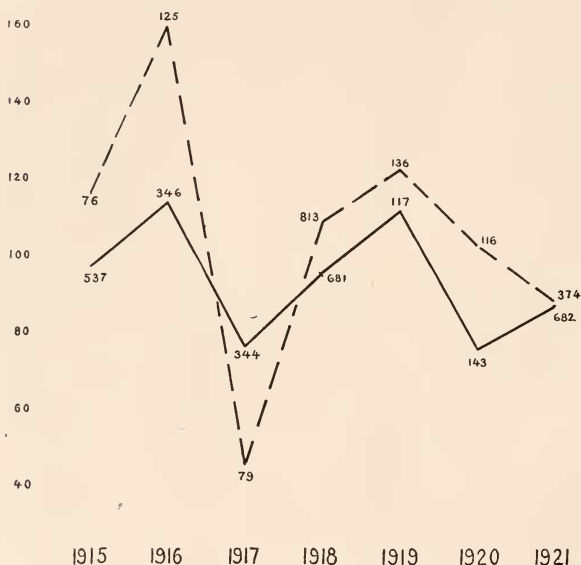

Fig. 7. Differences in the sex ratio during the different years comprised in our records. Continuous line = pure. Dotted line = hybrids.

the sex ratio for that month (based on the entire material). The weighted mean for the year in question was then computed. None of the yearly ratios thus obtained differed by more than 4.0 from the general ratio (97.37), showing that seasonal distribution cannot account for these yearly differences.

Nor are the latter to be accounted for by the possibly unequal distribution of pure and hybrid births. Figure 7 shows that the

same year-to-year fluctuations were undergone by both pure and hybrid stock, with the exception of the last (from 1920 to 1921).

When each of these years is divided into 3-month periods (February to April, etc.), we find that, on the whole, the years of low and high ratio show this tendency for each of the four " seasons." Graphs (not here reproduced) show that the " curve " for 1917, while undergoing closely similar fluctuations to that for the entire series, remains throughout far below the latter. Of the other two " low " years, 1921 remains throughout below the mean, while 1920 gives a lower ratio in three out of four of these periods. Of the two years which show ratios appreciably higher than the mean, each gives a " curve " which keeps far above the mean during three of the four seasons. The exceptions fall at different times in the two cases.

These considerations, while they add little to the evidence for the statistical reality of these yearly differences, show that the latter do not depend upon conditions which act primarily during any particular period of the year. To be sure, computations have been made which show that the departures of these yearly ratios from the mean condition occur preponderantly in the fall and winter months. This relation is probably due to chance, however, so that the figures need not be given here.

Similar differences have been recorded by a number of investigators between the sex ratios of different years for mankind, but so far as we know, these differences have not been discussed by them. They have been regarded as accidental, or at least as irrelevant and negligible. Thus in the study by the Pearls, already referred to, of the sex ratios of " pure " and " hybrid " races in the city of Buenos Aires, the authors confine their discussion to the apparently higher ratios which are found among offspring of mixed parentage. They quite overlook the fact, however, that the sex ratio of the entire population varies materially from one year to another, and that these yearly differences are in some cases both absolutely greater and statistically more certain than are those between the pure and hybrid elements of the population. Thus the ratio for the year 1900 is $97.0 \pm .90$, while that for 1904 is $105.4 \pm .95$. Each of these figures is based

upon over 20,000 births, and the difference is 6 times its probable error. Even greater and more "significant" differences are to be found in the yearly ratios of some of the separate population groups (in one case $8 \times$ P. E.), and it is of interest here to note that the years of high and low sex ratios do not tend to correspond in these various groups, but that they sometimes show exactly opposite conditions.

It is, of course, inconceivable that a difference of calendar year, as such, should have any more influence upon the sex ratios of mice or men than the phases of the moon or the conjunctions of the planets. It is likewise improbable that any mean difference in the weather from one year to the next, can be the responsible factor. For the meteorological differences between the most widely unlike years are small in comparison with the differences between the summer and winter seasons in any single year. But we have seen that these yearly variations of sex ratio may be even greater than the seasonal ones. Again, examination of the composition of the stock during these widely divergent years (say 1916 and 1917) gives no suggestion of a clue based upon considerations of this sort.

Huxley (1920) discusses a case in which a teleost fish produced, for nearly a year, three times as many females as males. Later, this ratio among the young produced changed to 2 females : 3 males for a few weeks, after which the numbers of the sexes became approximately equal and remained so for several years. Huxley believes it probable that in the first stage a certain proportion of the individuals having the zygotic formula XY became "somatic females" or "feminized males," and that such individuals produced X and Y eggs, which by fertilization gave rise in the next generation to an excess of males. A converse hypothesis might, of course, be invoked to explain the change in our stock, from a ratio of 125 in 1916 to one of 71 in 1917. But this is suggested merely as a remote possibility, justified only by the utter absence of any plausible scientific explanation to cover the case.

Finally, it should be urged that even highly improbable things sometimes happen, and that it is not impossible that our most

" significant " figures may result from chance. An illustration of
this fact, drawn from the experience of the senior author, is
worth recording here. Two series of mice had been subjected to
a difference of treatment which even the most ardent believer in
" sex determination " by physical agencies would not think of as
being effective in this connection. The difference was that in one
series the right sciatic nerve was cut, in the other the left. The
first 9 broods of " right " parentage consisted of 14 females and
no males. During the same period, 5 broods were born of
" left " parentage, consisting of 10 males and 4 females. Had the
attempt been made to influence sex by experimental procedure,
the result would have seemed highly satisfactory. Thus, the
chance of obtaining 14 individuals which were exclusively females
is only one in 16,384, and the " significance " of the results is
increased when we consider the high preponderance of males in
the contrasted group. Experiences such as this lead one to de-
mand higher statistical probabilities than are frequently accepted
as convincing.

Summary.

Data have been presented, based upon over 4,600 deer-mice of
known sex, which were born and reared in captivity, under tem-
perature conditions not far different from those existing in nature.
The following results seem to be of most importance.

1. In size the broods ranged from 1 to 9, the mean of the
1,567 broods being 3.22.

2. The sex ratio for the entire lot was 97.37 ± 1.93. When
we include only those broods in which no deaths are known to
have occurred (nearly nine tenths of the whole) the figure be-
comes 98.01 ± 2.07. Broods known to have been incomplete give
a ratio of 93.08 ± 5.25. In order to eliminate the effect of sea-
sonal differences, the mean of the monthly means has been com-
puted. This is 95.65. None of these figures can be regarded
as differing significantly.

3. The probable errors employed throughout this paper are
based upon a formula different from that which has been used by
various previous writers. As a result, the errors here given are
about twice as great as would formerly have been computed, and

the probabilities claimed by us are correspondingly lower. According to this safer criterion, some of the most interesting of our differences are not decisively " significant."

4. Considering our aggregate material, there seems to be a definite seasonal cycle in the proportion of males and females born. The sex ratio presents two annual maxima, in March–April and August–October, respectively; and two annual minima, in winter and summer, respectively. The lowest figure is 78.79 ($\pm$ 6.93), in November and the highest 113.04 ($\pm$ 8.04) in April. This difference is about 3¼ times its probable error, and would ordinarily be regarded as " significant." A well-marked biennial rhythm is shown by both pure and hybrid stock, taken separately, though the fall maximum occurs in different months in the two cases. On the other hand, when our material is subdivided in certain other ways, the results are in some cases highly contradictory. We cannot, therefore, regard the existence of a seasonal cycle in the sex ratio of *Peromyscus* as being proved conclusively by our data.

In any case, the position of these annual maxima and minima, as found by us, does not correspond with those which have been reported for the white rat or for man. Indeed, the conditions in *Peromyscus* are very nearly the reverse of those described by certain other authors.

5. Subspecific hybrids (1,722) give a mean ratio of 104.76 $\pm$ 3.41. Mice of " pure " race (2,930) give a mean ratio of 93.27 $\pm$ 2.32. Considering these figures alone, the difference is barely significant statistically, but its reality is borne out by various other considerations. Furthermore, such an effect of hybridization upon the sex ratio was to be expected in view of the findings of various other biologists, working upon widely different organisms. It is possible, also, that the several subspecies of *Peromyscus* differ *inter se* to some extent.

6. A positive correlation exists in our material between the size of the brood and the sex ratio. Broods containing one to three individuals give a mean sex ratio of 94.85 $\pm$ 2.94, ones containing four to nine individuals give a mean sex ratio of 102.42 $\pm$ 3.01. The magnitude of these probable errors raises the suspicion, however, that these differences are accidental, and

our doubts are further increased by the lack of a uniform grada-
tion when the broods are grouped according to size.

7. When the number of each possible combination of males
and females, in broods of each size, is compared with the num-
ber expected according to chance, the conformity is found to
be, on the whole, very close. For example, the number of all-
male and all-female broods (excluding broods of one) was 276,
the "expected" number being 274. There is thus no preponder-
ant tendency toward the production of homosexual litters, and
thus no likelihood that polyembryony or true twinning is at all
common in these animals.

8. In our material, the sex ratio is lower for the earlier broods
(91.7) than for later broods of the same mother (103.3). The
numbers are so small, however, that the difference is probably ac-
cidental.

9. Likewise, inbreeding and outbreeding seem to have had no
influence upon the relative numbers of males and females, within
the limited material available for this comparison.

10. Similarly negative results were obtained from a compari-
son of the offspring of meat-fed individuals with the offspring
of those whose diet was strictly vegetarian. Here again, the
numbers were too limited to permit us to regard this experiment
as decisive.

11. The most significant result of all, statistically speaking,
and one which is at present utterly inexplicable, is the fact that the
sex ratios for the seven different years included in our records show
a wide range of variation. The extreme figures are those for
1916 and 1917, the ratios being 125.36 ± 7.82 and 70.56 ± 4.70,
respectively. These figures are based upon 471 and 423 indi-
viduals, respectively. The difference is 54.80 ± 9.1 (*i.e.,* differ-
ence $= 6 \times$ P. E.). The likelihood of obtaining such a result by
"accident" is less than one in 40,000. We have furthermore
determined that this difference is not due either to the seasonal
distribution of births, to the preponderance of hybrid births in
one year, as compared with another, or to the operation of any
of the other factors previously considered.

Mention was likewise made of the occurrence of similar annual
differences in the sex ratio of man as revealed by the tables of

Pearl and Pearl (1908). Some of these differences we have shown to be much more highly "significant"—according to accepted standards—than the differences between the pure and hybrid races with which these authors were concerned.

DISCUSSION.

In a field as well tilled as that of sex determination, it is both impracticable and undesirable for us to enter into any extensive review of the literature, and we offer no apology for the inadequate references to other workers which we have found it possible to include in the foregoing pages. Those who are unfamiliar with the literature of this field are referred to works by Geddes and Thomson (1914), Marshall (1910), Morgan (1913), and Doncaster (1914). The last two of these books are of particular value in this connection and supplement one another very nicely, since the viewpoint of the authors differs rather widely.

In recent years the view has been gaining ground that the sex of the individual is determined by the chromatin constitution of one or the other of the germ cells. In the majority of cases which have been investigated, it is believed that the differential factor is contained in the sperm cell, though there is evidence in a number of instances that the ovum is the gamete concerned. The cytological and genetic data upon which these conclusions are based are too well known to be discussed here. For many organisms the evidence is doubtless wholly convincing.

Many well-attested cases exist, however, in which the sex ratio is known to be correlated with certain external factors. Those who wish to universalize the chromosomal theory of sex determination, dispose of such cases by assuming the existence of either a differential mortality among the developing organisms, or a differential mortality among the sex-determining gametes, or some other factor favoring one class of gametes or zygotes, as compared with the other. It is assumed by such biologists that the sex of the organism is invariably predetermined in the nucleus of the fertilized egg, and is not subject to reversal by any influence that can be brought to bear subsequently.[1]

[1] Morgan (1913), for example, devotes a section of a chapter to "The Abandoned View that External Conditions Determine Sex," though there are reasons for believing that Professor Morgan does not take such an extreme position at the present time.

Other biologists, while granting this absolute predetermination of sex for some organisms, believe that in other cases the condition of the nucleus may be neutral in this regard, and that which of two potentialities shall finally prevail may be determined by chemical or physical influences acting upon the developing organism. There is, indeed, evidence which seems irreconcilable with the view that sex is always predetermined in the nucleus of the fertilized egg. We think, accordingly, that this second position is the safer one in the present state of our knowledge.[2]

As regards the data here reported for *Peromyscus,* we believe that (granting the reality of certain of the differences found) they lend themselves perhaps equally well to either of the above conflicting viewpoints. There may, for all we know, be seasonal differences in the relative production of male-producing and female-producing spermatozoa. Or, one kind may be more active at one time of the year than another. Or, the ova may so vary in their chemical composition that their attractive influence upon one or another type of spermatozoön varies with the season. Any or all of these things may be true, though there is not a scintilla of evidence that such is the case.

As regards the effect of crossing upon the sex ratio, this too, is reconcilable with either viewpoint. There might, in one way or another, be a preponderant selection of male-producing spermatozoa in hybrid fertilizations. On the other hand, the increased vigor which frequently accompanies hybridization might well influence the metabolism of the parents, and thus affect that of the developing fetuses.

When we come to those fluctuations in the sex ratio which are met with from one year to another, we must admit that their causes are utterly obscure. In the case of *Peromyscus,* it is difficult to conceive of any scientific explanation whatever for the fluctuations found. Even when we admit the likelihood that environmental conditions may play a direct or indirect part in sex determination, it is hard to see how the relatively slight differences which distinguish one year from another could bring about a greater effect than the vastly larger differences which distinguish the seasons of a single year. The calendar year, as such, would

[2] This is the viewpoint adopted by Doncaster (1914, Chapter X.).

seem to be as devoid of causal efficacy in this matter as are the planetary influences which are invoked by the astrologists.

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